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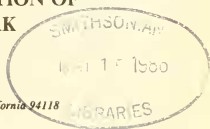
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BILATERAL ASYMMETRY IN PHALLOSTETHID FISHES
(ATHERINOMORPHA) WITH DESCRIPTION OF
A NEW SPECIES FROM SARAWAK

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ABSTRACT: *Phenacostethus trewavasae*, the first phallostethine from Borneo, is described from clay- and gravel-bottom freshwater streams of the Baram River, Sarawak. One of the distinguishing characteristics of *P. trewavasae* is a minute eye-lens. The subfamily Phallostethinae comprises *Phallostethus* Regan, known only from a single collection of one species; *P. dunckeri* Regan, from the mouth of the Muar River, in Johore on the Malay Peninsula; and *Phenacostethus* Myers, known previously from two species, *P. smithi* Myers and *P. posthon* Roberts, from coastal peninsular Malaysia and Thailand.

Male phallostethids are bilaterally asymmetric. The subcephalic copulatory organ, the priapium, is oriented so that the apical side of the body is either the left or right; hence, males are termed sinistral or dextral, respectively. Both *Phallostethus dunckeri* and *Phenacostethus smithi* have, in about equal numbers, males that are either sinistral or dextral. In *P. posthon*, all males are dextral, whereas, in *P. trewavasae*, all males are sinistral. One species of neostethine, *Mirophallus bikolanus* Herre, is known in which all males are dextral.

Bilateral asymmetry is compared among phallostethids to assess better the nature of this phenomenon, and its importance in determining the homology of priapial structures.

INTRODUCTION

Phallostethids are a group of some 20 known species of Indo-Australian atherinomorph fishes distinguished from all other teleosts by the presence in males of the priapium, a complex, subcephalic copulatory organ (Regan 1913, 1916). Phallostethids have been divided into two groups (and classified traditionally in two families, Phallostethidae and Neostethidae, as in Roberts 1971a, b) on the basis of gross differences in priapial morphology. Rosen and Parenti (1981) and Parenti (1984) treated the entire group as one family, the Phallostethidae sensu lato, and that convention is followed here; the two groups are referred to as the subfamilies Phallostethinae

and Neostethinae. The closest living relative of the freshwater, brackish, and occasionally salt-water phallostethids is hypothesized to be the monotypic western Pacific marine silverside (or hardyhead) *Dentatherina* Patten and Ivantsoff (Parenti 1984).

The subfamily Phallostethinae includes two genera: *Phallostethus* Regan with one species, *P. dunckeri* Regan, 1913, and *Phenacostethus* Myers, with three species, *P. smithi* Myers, 1928, *P. posthon* Roberts, 1971a, and *P. trewavasae*, described herein.

Phallostethids are found throughout coastal peninsular Malaysia, Thailand, Borneo, the Philippines, and Java. *Phallostethus* and *Phenacostethus* were known previously only from penin-

sular Malaysia and Thailand (see Roberts 1971a, fig. 1). The third species of *Phenacostethus*, *P. trewavasae*, was collected from the Baram River in Sarawak, Malaysian Borneo. Fowler (1937) described *Phenacostethus thai* from a series of nine specimens, four males and five females (Academy of Natural Sciences, Philadelphia, ANSP 51352–51360). Roberts (1971a) followed Herre (1942) in treating *Phenacostethus thai* as a synonym of *Phenacostethus smithi*, and I tentatively concur.

All Phallostethinae and Neostethinae males are bilaterally asymmetric with regard to orientation of the major supporting bones and other structures associated with the priapium. Most females are bilaterally symmetric; the anus is just anterior to the urogenital opening along the ventral midline, under the throat (see Regan 1913, fig. 2). In just one species of neostethine are bilaterally asymmetric females found (see Parenti, in press).

Bilateral asymmetry is well documented in fishes (see Hubbs and Hubbs 1945, and references therein, for a comprehensive review). Most phallostethid species have both sinistral and dextral males in more or less equal numbers. Roberts (1971a) described *Phenacostethus posthon*, the first known species in which males are exclusively dextral. *Phenacostethus trewavasae* males are exclusively sinistral. Both species are known from relatively large numbers of specimens, such that unique or fixed asymmetry can only be interpreted as a natural phenomenon in some phallostethids.

Phenacostethus trewavasae is also distinguished by a minute eye-lens. The structure and function of the retina and, hence, the quality of vision, is unknown.

MATERIALS AND METHODS

The material on which the description of *Phenacostethus trewavasae* is based was made available for study by Dr. E. J. Crossman, of the Royal Ontario Museum (ROM), where the holotype and majority of paratypes and additional specimens are deposited. Remaining paratypes have been deposited in the California Academy of Sciences (CAS), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), and the United States National Museum of Natural History (USNM), through the courtesy of Dr. Crossman.

Included in the comparative material are specimens of *Phallostethus dunckeri* Regan from the single known collection by G. Duncker from the Muar River, in Johore on the Malay Peninsula (Duncker 1904). Regan's (1913) description was based on seven specimens from this collection. Both Roberts (1971b) and Parenti (1984) believed that the only known specimens were the BMNH syntypes. However, additional specimens from the single collection by Duncker have been discovered in the Zoologisches Museum, Hamburg (ZMH) and have been made available for study through the courtesy of Prof. H. Wilkens. Some of the ZMH material was given lectotype and paralectotype status erroneously by Ladiges et al. (1958), who did not refer to the BMNH syntypes.

Osteological structures were examined in, and counts made on, material counterstained with alcian blue and alizarin red S following the procedure of Dingerkus and Uhler (1977), or solely alizarin stained. See text and Table 2 for catalog numbers of phallostethid material examined. Alcohol-preserved (USNM 230367, USNM 230181), solely alizarin-stained (USNM 230371, USNM 230366), and counterstained preparations (USNM 230374) of the western Pacific *Dentatherina merceri* were used for outgroup comparison. Additional comparative material was obtained on loan from the University of Michigan, Museum of Zoology (UMMZ) and the Museum of Comparative Zoology, Harvard University (MCZ).

A Zeiss SV8 stereomicroscope with drawing tube and photomicrography apparatus was used for dissection of specimens and recording of data.

Phenacostethus trewavasae, new species

(Figures 1–3, 4b)

HOLOTYPE.—ROM 41826, a mature, sinistral male, 14.1 mm standard length, collected 3 August 1981, by Dwight Watson, from Malaysia: Sarawak (Fourth Division), Baram River, Sungai Kejin Tugang, tributary of Sungai Kejin, depth to 1 m, clay- and gravel-bottom stream (03°41'30"N, 114°27'15"E).

PARATYPES.—ROM 44289 (8 sinistral males, 11 females); ROM CS 812 (2 sinistral males, 1 female, all cleared and stained with alizarin red S); ROM 41827 (1 adult female), taken with the holotype.

ROM 41829 (1 sinistral male); ROM 41830 (7 sinistral males, 6 females); CAS 55454 (3 sinistral males, 2 females); BMNH 1984.7.12:1–5 (3 sinistral males, 2 females); AMNH 55570 (3 sinistral males, 2 females); USNM 267266 (2 sinistral males, 3 females), all collected 11 February 1980, by Dwight Watson, from Malaysia: Sarawak (Fourth Division), Baram River, Sungai Kejin, station at confluence of Kejin Tugang and Kejin

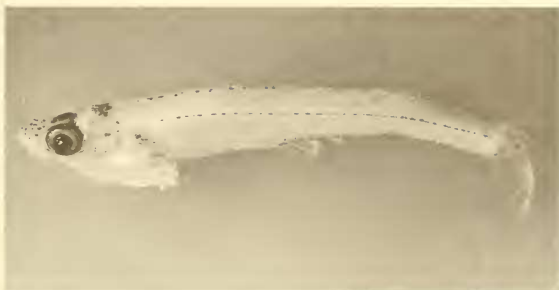


FIGURE 1. *Phenacostethus trewavasae*, 14.1-mm holotype (ROM 41826).

River, depth to 1 m, clay- and gravel-bottom stream, no vegetation (03°41'30"N, 114°27'15"E).

ADDITIONAL MATERIAL EXAMINED (no type status).—ROM 41828 (11 juveniles), collected 27–30 July 1981 from Malaysia: Sarawak (Fourth Division), Baram River, Loagan Titad.

ROM 44290 (9 sinistral males, 17 females, 3 juveniles or of undetermined gender, of which 2 sinistral males and 2 females have been counterstained with alcian blue and alizarin red S); ROM 44291 (24 sinistral males, 12 females, 14 juveniles or of undetermined gender) taken with the holotype.

DIAGNOSIS.—*Phenacostethus trewavasae* is distinguished from its sister species, *P. posthon*, by having only sinistral males, that is, with apbroctal side of body on the left. The hooklike

toxactinium arises on right side of head and curves very strongly under head towards left side of body. Males of *P. posthon* are exclusively dextral. Four characters distinguish the sister species from *Phenacostethus smithi*: distal portion of penis smooth; penial bone absent; ctenactinium small or absent; and stout and distinctly curved, hooklike toxactinium (see Fig. 5). Males of *P. smithi* are either sinistral or dextral and occur in about equal numbers (see Introduction, Relationships, Bilateral Asymmetry, and Table 2).

A second diagnostic character is a minute eye-lens (Fig. 4b), as compared with the relatively large eye-lens of *P. posthon* and *P. smithi* (Fig.



FIGURE 2. *Phenacostethus trewavasae*, left lateral view of head and anterior portion of body of 14.1-mm holotype (ROM 41826).

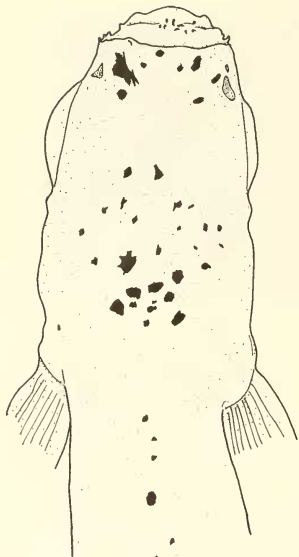


FIGURE 3. Diagrammatic representation of dorsal melanophore pattern, *Phenacostethus trewavasae*, male paratype (ROM 44289).

4a), more typical of that found in diminutive teleost fishes (see below).

DESCRIPTION.—Slender, laterally compressed diminutive phallostethid fish, distinguished by minute eye-lens and by males with sinistral priapium. *Phenacostethus trewavasae* like congeners in meristic data (Table 1). No vestigial pelvic fin rays or supports in females; males with pelvic and parts of pectoral fins modified into priapium that is invariably sinistral: prominent externalized subcephalic bone a toxactinium arising on right side of body, articulating with right axial bone, and curving strongly under head towards left side of body (Fig. 4b). Cartilaginous pulvinular pad lateral to and covering articulation point of, toxactinium and axial bone; small antepleural bone just posterior to point of articulation. Mi-

nute ctenactinium articulates with posterior base of right axial bone. Penis smooth not ruffled as in *P. smithi* (see Roberts 1971a). Pleural ribs of fifth? vertebra, each with a posterior flange, elongate dorsoventrally, meeting just dorsal to right axial bone (Fig. 4a). First pleural rib on fourth vertebra in females, fifth vertebra in males.

Skull, gill arches, and jaws like those illustrated for *Phallostethus dunckeri* Regan by Parenti (1984), with following qualifications. Frontals project above dorsal head profile (Fig. 1, 2, 4b). Three infraorbital bones: preorbital, second infraorbital, and dermosphenotic. Outer jaws with few unicuspid teeth; parodontary with cartilaginous core and slight perichondral ossification, no teeth. Lower jaw protrudes beyond anterior extent of upper jaw. Submaxillary element cartilaginous. Rostral cartilage pear-shaped, wider posteriorly. Two small accessory cartilages between medial ramus of maxilla and rostral cartilage (as in *Ceratostethus bicornis*, Roberts 1971b, fig. 5). Gill arch skeleton highly cartilaginous. Unicuspid teeth on fourth ceratobranchial and infra-pharyngobranchial toothplates. Three cartilaginous basibranchials posterior to cartilaginous basihyal.

Caudal skeleton with two epurals and autogenous parhypural. Caudal fin forked, dorsal and ventral rays forming incipient lobes. Pectoral fin narrow and elongate. Two dorsal fins, the first with a single spine or ray supported by single pterygiophore.

Ventral dermal keel extending from base of priapium in males or urogenital opening in females, to anal fin origin.

Scales on body small and deciduous, absent from dorsal surface of head. Color pattern in alcohol similar to that of congeners (as in Roberts, 1971a, confirmed by personal observation): melanophores scattered on dorsal surface of head and anterior portion of body (Fig. 3), along mid-lateral intermuscular septum, around orbit, on operculum and priapium, and along basal portion of anal fin, dorsal midline, and ventral midline. Ground coloration very pale yellow or light brownish in alcohol; coloration in life unknown, although *P. trewavasae* is probably nearly translucent in life, as are its congeners. Largest specimens reported by Roberts (1971a:13–14) of *P. posthon* and *P. smithi* with a bright orange yellow bar on caudal peduncle and a smaller orange yellow bar on the body “next to the anal fin origin.”

ETYMOLOGY.—*trewavasae*, in honor of Dr. Ethelwynn Trewavas, British Museum (Natural History), to express my deep appreciation of her continued contribution to the field of ichthyology.

EYE-LENS SIZE

The eye-lens is a nearly perfect sphere at the center of the eyeball (Fig. 4). In *P. trewavasae* (Fig. 4b), the eye-lens is minute compared with that of *P. smithi* (Fig. 4a). A minute eye-lens has been observed in all seven of the cleared and stained specimens of *P. trewavasae*. Four of these specimens were chosen at random from a lot of alcohol-preserved specimens for study: a mature male, an immature male, and two adult females (ROM 44290) that were counterstained for bone and cartilage. Three of the seven specimens—two mature males and one adult female (ROM CS 812)—stained solely with alizarin, were not prepared by me, but were probably chosen at random for preliminary identification at ROM. The presence of a minute eye-lens has been confirmed, by dissection, in alcohol-preserved specimens. Size of the eye-lens varies from minute to barely detectable with a dissecting microscope, so that the character of a minute eye-lens may represent a stage in a transition series from a small eye-lens to eye-lens absent.

The ratio of the distance between the center of the lens and the retina to the radius of the lens is nearly a constant in adult teleost fishes. This constant of 2.55, known as Matthiessen's ratio, has been demonstrated in numerous teleosts, and has been confirmed in the cichlid *Haplochromis elegans* Trewavas (Otten 1981). During growth of *H. elegans*, the ratio increases rapidly from about 2.2 to 2.8, then decreases slowly to about 2.5 before leveling off at about 2.55 in the adult (Otten 1981, fig. 15).

Matthiessen's ratio in *P. trewavasae* could not be measured directly as part of this study. However, a minute eye-lens at the center of the eyeball and a normal retina will not affect the distance from the center of the lens to the retina. But, obviously, Matthiessen's ratio will be greatly increased by a small eye-lens radius, and the distance from the center of the lens to the retina will be greater than the focal-length of the eye-lens.

Visual acuity at any given stage in ontogeny is a function of retinal structure as well as shape of

the eyeball (Otten 1981; Levine and MacNichol 1982; Fernald 1985). Growth of the eye-lens is probably retarded very early in ontogeny. Structure and function of the retina, as well as other accommodation made during ontogeny for a minute eye-lens, is unknown. Without such information, the quality of natural vision in *P. trewavasae* will remain open to speculation, but several statements can be made.

First, *P. trewavasae* may have poor visual acuity simply because of the optical properties of a minute eye-lens (Kirschfeld 1976). The short focal length of the eye-lens can be correlated with low resolving power, decreased ability to distinguish among wavelengths of light, and high chromatic aberration. In very small lenses, absolute aperture limits resolving power (Otten 1981:681).

Second, *P. trewavasae* lives in clay- and gravel-bottom, freshwater streams of the Baram River, Sarawak. The species is apparently omnivorous, with sample gut-contents including, for example, larval or juvenile *P. trewavasae* and adult dipterans. Field notes state that there was no vegetation at *P. trewavasae* collecting sites. If the minute eye-lens limits the visual acuity of *P. trewavasae*, then we may assume that the species does not seek out prey visually.

RELATIONSHIPS

Myers (1928) distinguished *Phenacostethus* from *Phallostethus* by a shorter anal fin (Table 1), a protruding lower jaw, and the absence in the female of a groove on the abdomen. Regan (1913, 1916) did not state whether *Phallostethus dunckeri* has a spinous first dorsal fin, and Myers (1928) and Roberts (1971a, b) could only speculate about its presence. The first dorsal fin is absent in the syntypes in the BMNH (Parenti 1984) and absent in the material in the ZMH.

Further, Myers (1928) said that *Phenacostethus* resembled *Phallostethus* and differed from *Neostethus* (and, in fact, from all Neostethinae) in having a priapium that has a prominent hook-like anterior element (the toxactinium) and a shieldlike pulvinular pad. Nevertheless, these elements, or their homologs, are present in most phallostethids. They are well developed and hence are the prominent priapial elements in *Phallostethus* and *Phenacostethus*.

Division of phallostethids into two groups emphasized gross differences between the types of priapia. However, no assessment of whether one

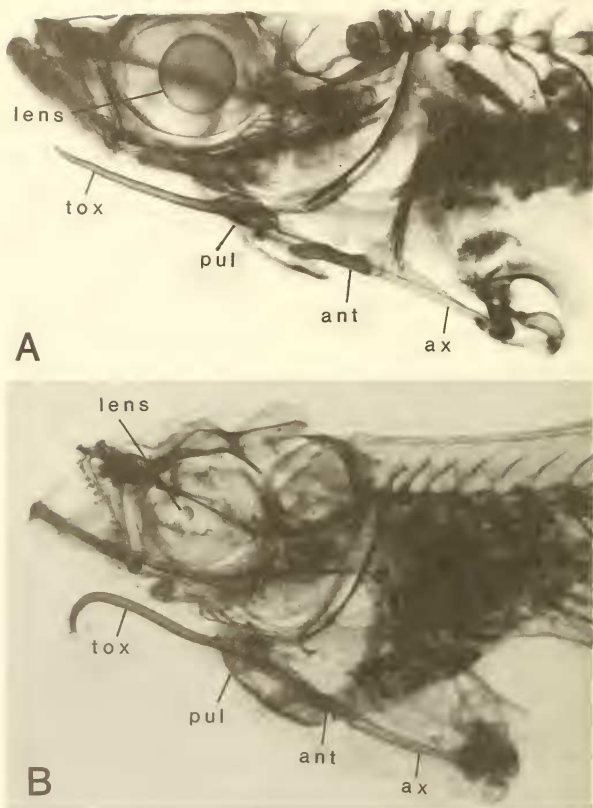


FIGURE 4. Left lateral view of head and anterior portion of body of cleared and stained preparations of male a. *Phenacostethus smithi* (MCZ 47299), and b. *Phenacostethus trewavasae* (ROM 44290), focused on eye-lens. Abbreviations: tox = toxactinium; pul = pulvinular pad; ant = antepleural; ax = axial bone.

or both represented a derived priapium has been incorporated into a classification. For example, Roberts's (1971b:396) branching diagram of phallostethid genera clearly indicates a paraphyletic Neostethinae. Furthermore, he interprets the neostethinae priapium as primitive (Roberts 1971b:395): "The priapium of Neostethinae, in which the only externalized elements are derived from pelvic spines and rays, is evidently more primitive than [the priapia of all other phallostethids]."

Phallostethus and *Phenacostethus* together can be defined as monophyletic by the following shared derived characters (some characters modified from Roberts 1971a:5-6; his numbering not followed):

1. Slender, elongate atherinomorph fishes, with deciduous scales; diminutive—maximum standard length recorded 17.0 mm (Roberts 1971a).

2. Body translucent or transparent, melanophores scattered on top of head (Fig. 3), middle of dorsum, midlateral intermuscular septum, priapium, and basal and distal portion of fin rays (Fig. 1, 2).

3. Dorsum of head with translucent, membranous dome (not as noticeable in alcohol-preserved specimens owing to dehydration).

4. Teeth on premaxilla, parodontary, and dentary small, fewer in number than in other phallostethids and atherinomorphs; no large outer teeth on lateral ramus of premaxilla.

5. Main externalized bone of priapium a toxactinium (Regan 1916; Myers 1928).

6. Large, oval, concave, cartilaginous pulvinular pad covering point of articulation of toxactinium with axial bone (Regan 1916; Myers 1928).

7. Coiled vas deferens terminates in fleshy genital pore or penis that projects from posterior section of priapium.

8. Pelvic spines or rays reduced or absent.

9. Vas deferens highly coiled, forming what has been termed an "epididymus" (Regan 1913, 1916).

Most of these characters represent reductions; that is, we might think of *Phallostethus* and *Phenacostethus* as diminutive phallostethids that, perhaps because of small size, have lost or reduced characters such as pelvic spines and fin rays, complete squamation and heavy pigmentation, and more complete, fuller outer dentition. However, the priapium of *Phallostethus* and *Phenacostethus* cannot be regarded as a reduced

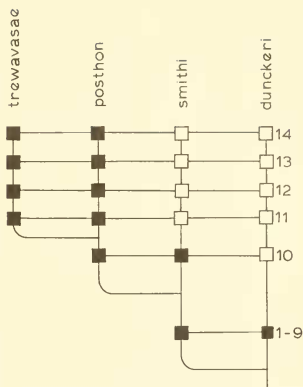


FIGURE 5. Cladogram of relationships among the four species of *Phallostethus* and *Phenacostethus*. Black squares represent one or more synapomorphies; open squares represent one or more symplesiomorphies. Character 1) slender, elongate, diminutive fishes with deciduous scales; 2) body translucent or transparent, melanophores scattered on top of head, middle of dorsum, midlateral intermuscular septum, priapium, and basal and distal portion of fin rays; 3) dorsum of head with translucent, membranous dome; 4) teeth on premaxilla, parodontary and dentary small; 5) main externalized bone of priapium a toxactinium; 6) large, oval, concave, cartilaginous pulvinular pad covering point of articulation of toxactinium with axial bone; 7) coiled vas deferens terminates in fleshy genital pore or penis; 8) pelvic spines or rays reduced or absent; 9) vas deferens highly coiled; 10) protruding lower jaw; 11) distal portion of penis smooth; 12) penial bone absent; 13) ctenactinium small or absent; 14) stout and distinctly curved hooklike toxactinium. See text for defining characters of each species.

character complex. Several elements, including the pulvinular and the externalized toxactinium (homologous with the internalized secondary pulvinular; Roberts 1971b), are more well developed than in other phallostethids. The fact that pelvic fin rays at the base of the priapium are absent in *Phallostethus* and *Phenacostethus*, whereas rudimentary rays are present in neostethines, is interpreted as a derived condition representing a further modification of the pelvic fin supports and rays.

Relationships among the four species of phallostethines are summarized in the cladogram in

TABLE 1. MERISTIC CHARACTERS OF *PHALLOSTETHUS* AND *PHENACOSTETHUS*

	First dorsal rays	Second dorsal rays	Anal rays	Pectoral rays	Branchiostegal rays	Vertebrae
<i>Phallostethus dunckeri</i>	0	8-10	26-28	9-10	4	40
<i>Phenacostethus trewavasae</i>	1	6	14-15	9-10	5	34
<i>Phenacostethus posthon</i>	1	5-6	14-15	9-10	4	34-35
<i>Phenacostethus smithi</i>	1	6-7	14-15	9-11	4-5	33-35

Figure 5. *Phallostethus* is readily defined by its extremely long anal fin, relatively high number of vertebrae (Table 1), serrated ctenactinium (Regan 1913), and absence of the first dorsal fin (Parenti 1984). The last two characters are also found in some neostethines.

Phenacostethus is defined as monophyletic by the protruding lower jaw (Myers 1928). Myer's additional character, absence of a groove on the abdomen of females, seems to be correlated with quality of preservation, and therefore is not used here.

Phallostethus and *Phenacostethus* are not synonymized here solely for reasons of tradition.

Phenacostethus trewavasae resembles *P. smithi* in that the first and second dorsal fins are separated by a relatively large distance, as opposed to being rather close together, as in *P. posthon* (see Roberts 1971a, fig. 2, 3). The distance between the first and second dorsal fin is a primitive character in *P. smithi* and *P. trewavasae*, and serves as a defining character of *P. posthon*.

Roberts (1971a) described *P. posthon* as reduced in a number of character states relative to *P. smithi*, then its only congener. Three character states that may be described as shared reductions in *P. posthon* and *P. trewavasae* are: (1) distal portion of penis smooth, as opposed to being

ruffled as in *P. smithi*; (2) penial bone absent; (3) ctenactinium, if present, small and barely detectable. These characters were illustrated in both *P. posthon* (Roberts 1971a, fig. 6) and *P. smithi* (Roberts 1971a, fig. 7). (Figures and captions were switched inadvertently when printed, as noted in a published erratum.)

These three reductions are considered synapomorphies of *P. posthon* and *P. trewavasae*. They are correlated with a stouter and more distinctly curved hooklike toxactinium (compare Fig. 4a and 4b). Thus, even though the two species have characters that can only be described as reductions, these characters are treated as synapomorphies in phylogenetic reconstruction because of their correlation with uniquely derived characters (Fig. 5).

BILATERAL ASYMMETRY

A. Anatomical Homology

Bilateral asymmetry is well documented in fishes (Hubbs and Hubbs 1945). The phenomenon usually concerns reproductive structures offset to, or more complex on, one side of the body; although, the well-known asymmetry of flatfishes (pleuronectiforms) is not necessarily associated with reproduction.

TABLE 2. BILATERAL ASYMMETRY IN FIVE SPECIES OF PHALLOSTETHIDAE (SENSU LATO)

	Total	Dextral males	Sinistral males	Females	Juveniles or undetermined
<i>Phallostethus dunckeri</i> (a)	25	4	1	16	4
<i>Phenacostethus trewavasae</i> (b)	148	0	63	57	28
<i>Phenacostethus posthon</i> (c)	237	107	0	99	31
<i>Phenacostethus smithi</i> (d)	334	179	155	0	0
(e)	31	4	6	10	11
<i>Mirophallus bikolanus</i> (f)	300	173	0	108	19

(a) BMNH 1913.5.24:18-20,21,22, ZMH 193-195; (b) total of known specimens, catalog numbers in text; (c) MCZ 47300, 47301 A,B, USNM 229302; (d) Hubbs and Hubbs 1945:290, table XIX; (e) BMNH 1927.12.29:1-10; (f) AMNH 50592, CAS 50722, CAS 53165, UMMZ 211665.

Regan (1916:23) was the first to use the terms "sinistral" and "dextral" to refer to the orientation of the priapium: "In its asymmetry and in being either dextral or sinistral the priapium agrees with the copulatory organ of *Anableps*," a possibly bilaterally asymmetric killifish genus (see Hubbs and Hubbs 1945:289–291). According to the convention established by Regan, in a sinistral male, the anal opening is on the right, what he termed the "proctal side." Hence, the left side of a sinistral male is termed the "aproctal side." The opposite is true for a dextral male, which may be thought of as the mirror image of a sinistral conspecific male. All female phallostethines examined exhibit no bilateral asymmetry; the anus is just anterior to the urogenital opening along the ventral midline under the throat. (See Parenti in press for report of bilateral asymmetric females in one neostethine species.) Regan (1916:21) also pointed out marked differences between priapia of phallostethines and neostethines: "The approximate symmetry of the priapial ribs and cleithra in *Phallostethus*, as compared with their marked asymmetry in *Neostethus*, is no doubt due to the symmetrical attachment of the priapium in the former . . . and its asymmetrical attachment . . . in the latter."

Proportions of sinistral and dextral males of *Phenacostethus smithi* were shown to be equal (Hubbs and Hubbs 1945; Table 2, herein). It was assumed that, with sufficient sample sizes, phallostethid species would be represented by more or less equal numbers of sinistral and dextral males, until Roberts (1971a) described *Phenacostethus posthon*, an exclusively dextral species.

Roberts (1971a) termed *P. posthon* sinistral. However, it is more properly called dextral in keeping with homologies of priapia among all phallostethids. Confusion about whether to call a male sinistral (a left) or dextral (a right), may be traced to a casual statement by Myers (1928: 5): "The proctal side may be indifferently either the right or the left of the fish; in other words, the males are either 'rights' or 'lefts.'" In interpreting this statement strictly, one would assume Myers meant that a male with the proctal side on the right should be called a dextral, or a right. However, this is contrary to the terminology established by Regan and followed by most phallostethid systematists (e.g., Herre 1942; and Myers 1928 himself). Regan emphasized that the proctal side was away from the female during

copulation, and that the aproctal side, the side with the fleshy genital pore or penis, was the obviously functional side of the male with regard to internal fertilization (see also Villadolid and Manacop 1934).

Herre (1942:139) followed Regan's convention but was ambiguous when describing asymmetry: "The coiled, enlarged vas deferens lies within the posterior end of the priapium, from which its penis-like tip projects. The proctal side may be either side, so that males of the same species may be either 'rights' or 'lefts.'" Hubbs and Hubbs (1945:290, table XIX) followed Regan strictly and documented bilateral asymmetry by tabulating the "location, left (L) or right (R), of aproctal side of males of Phallostethidae *Phenacostethus smithi*."

Division of phallostethids into two families was based primarily on the type of prominent external priapial bones. Phallostethines have a hooklike toxactinium that articulates with the axial bone (Fig. 4), a homolog of the pelvic fin girdle (Bailey 1936; Aurich 1937), and curves underneath the head toward the aproctal side (Regan 1916; Herre 1942; Fig. 2, 4 herein). Hence, a male phallostethine with a toxactinium arising on the right side of the head and curving toward the left, aproctal side, is called sinistral because the aproctal side is the left. Such sinistral phallostethine males also have a rudimentary ctenactinium that articulates with the left, aproctal axial bone at its posterior extent.

The prominent externalized priapial bones of neostethines are the one or two ctenactinia that arise on the aproctal side of the body. Hence, a male neostethine with one or two ctenactinia arising on the left side of the body is termed sinistral not because of the position of these prominent priapial bones, but because the aproctal side is the left. This terminology should be adhered to strictly because of the consistency with the inferred homology of priapial structures. Furthermore, this convention for describing bilateral asymmetry of male phallostethids should be followed because the division between phallostethines and neostethines is not supported by unambiguous, derived characters.

Roberts (1971a:13), in describing *Phenacostethus posthon*, was explicit in describing bilateral asymmetry: "... the priapium is invariably sinistral (toxactinium arising on left side) in the material examined." It is clear, therefore, that

Roberts did not follow the convention established by Regan. Hence, I recommend that *P. posthon* be referred to as an exclusively dextral species, not sinistral as Roberts described it. This correction need not be made to Roberts's (1971b) discussion of the anatomy of *Ceratostethus bicornis* (Regan) because that species is a neostethine and the prominent external priapial bones are the ctenactinia, which arise on the aproctal side in every known example.

B. Unique or Fixed Asymmetry

Of the 148 known specimens of *Phenacostethus trewavasae*, 63 are sinistral males, 57 are females, and 28 are juveniles or of otherwise undetermined gender (see Diagnosis and Table 2). The collection of large samples of the exclusively sinistral *Phenacostethus trewavasae* allows us to conclude with certainty that unique or fixed asymmetry is a natural phenomenon in some phallostethids. In addition to the phallostethines *P. trewavasae* and *P. posthon*, the neostethine *Mirophallus bikolanus* Herre has males of fixed asymmetry (Tyson R. Roberts, personal communication). Three large lots of *M. bikolanus*, all collected from the Cabangan River, Albay Province in the Bicol (Bikol) region of Luzon, Philippine Islands, contain dextral males only. Of 300 specimens, 173 are dextral males, 108 are females, and 19 are juveniles or of undetermined gender (Table 2). The relatively high number of male and low number of juvenile or undetermined *M. bikolanus* is probably related to the fact that immature males are readily identifiable as such by the presence of a heavily pigmented anal region.

Unique or fixed asymmetry is a natural phenomenon in other atherinomorph fishes, as reviewed by Hubbs and Hubbs (1945). Females of the ricefish *Horaichthys setnai* Kulkarni may be considered sinistral in that the urogenital opening is to the left of the midline in a majority of females, and the right pelvic fin girdle and rays are absent in females (Kulkarni 1940; Hubbs 1941). Males of *H. setnai* have an anal fin modified into an elaborate gonopodium that is not bilaterally asymmetric as far as known. The viviparous poeciliids, *Carlhubbsia kidderi* (Hubbs) and *Xenodexia ctenolepis* Hubbs have a concavity on the right side of the gonopodium (Hubbs and Hubbs 1945). Males of the latter species also have a right pelvic fin modified into a so-called

"pectoral clasper" (Hubbs 1950), and a "... thickened fleshy ridge along the ventromesial edge of the proximal third of the outer ray of the right pelvic fin" (Rosen and Bailey 1963:143).

Phenacostethus posthon and *P. trewavasae* are sister species, the males of which are nearly mirror images of each other. Apart from type of bilateral asymmetry, they differ in several characteristics of priapial structure, placement of fins, and relative size of eye-lens (see Diagnosis, Description, and Relationships). One might assume that the common ancestor of these sister species, like most other phallostethids, contained both sinistral and dextral males (Fig. 5). One might assume further that it was the separation of the ancestral species into a sinistral and dextral population that precipitated (or, in fact, was) the speciation event. The problem with such a speciation hypothesis is that it presents a series of untestable statements, the first concerning states of the ancestral species, the second concerning isolation of sinistral and dextral subgroups.

Experimental data are needed to answer the questions: What is the genetic basis of bilateral asymmetry in phallostethids? Does a male phallostethid determine type of bilateral asymmetry of offspring? That is, does a sinistral male have only sinistral male offspring, and likewise, does a dextral male have only dextral male offspring? Breeding experiments to answer these questions, performed when live phallostethids are available for study, will further our understanding of the evolution of bilateral asymmetry, and the special case of fixed or unique asymmetry, in phallostethids.

CONCLUSIONS

Phenacostethus trewavasae new species, is described from the Baram River, Sarawak. It is the first phallostethine species known from Borneo. This subfamily had been reported previously from Thailand and peninsular Malaysia.

Two characters distinguish *P. trewavasae* from all other phallostethines: a minute eye-lens and males that are exclusively sinistral with regard to orientation of priapial structures. We may hypothesize reduced visual acuity in *P. trewavasae* because of the size of the eye-lens; however, a clear statement on vision awaits knowledge of structure of the retina.

All phallostethid males are bilaterally asymmetric, described by position of the anus: in si-

nistral males, the aprectal side is the left; in dextral males, the aprectal side is the right. Females exhibit no apparent asymmetry.

In most species, sinistral and dextral males are represented in more or less equal numbers. Sample sizes of the exclusively sinistral *Phenacostethus trewavasae* and the exclusively dextral *P. posthon* and *Miropallus bikolanus* allow us to conclude with certainty that unique or fixed asymmetry is a natural phenomenon in some phallostethids.

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